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Carabid Diets and Food Value

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Introduction

Carabid beetles are the dominant ground-living invertebrate predators in many ecosystems. Because of their often considerable size and their potential role in food-web dynamics and pest control, the food and feeding habits of carabid beetles may have been investigated in more detail than of any other group of predatory arthropod. This is also evidenced by numerous reviews (Forbes, 1883; Lindroth, 1949/1992; Thiele, 1977; Hengeveld, 1980b,c; Dajoz, 1987; Luff, 1987; Lövei and Sunderland, 1996) and extensive compilatory works (e.g. Larochelle, 1990). Feeding type, overall morphology and habitat choice show great variation (Forsythe, 1982a, 1983, 1987, 1991; Evans and Forsythe, 1985) and have led to the creation of extensive life form classifications (Sharova, 1981). A diversity of feeding specializations has been recognized. The most important deviation from the basic generalist predatory life style is the predominantly granivorous feeding of many species, but specializations to various animal prey have also been extensively described. In spite of the amount of work already done, there are numerous gaps in our knowledge and understanding, even as concerns common, relatively well-studied and economically important species. This review will build on the framework of feeding types established by earlier reviewers based on studies of stomach contents and natural history observations, but also focus on recent results concerning the quality of various food types to carabids with different feeding habits and specializations. Aspects related to food quantity (availability) will be largely neglected. The approach will expose large fields of research which have not previously been investigated. The review will concentrate on temperate species mostly from agricultural or forest habitats, whereas 'exotic' specializations in all senses of the word will also be neglected.

Few, if any, carabid species have diets restricted to a single food type or prey taxon: they are all polyphagous to various degrees. Preferences and adaptations to certain types of food have anyway evolved. These feeding specializations should be understood in a relative sense. Species have adapted to obtain the greater part of their food from a restricted range of food types that probably allow them to maintain a high fitness ('essential food'). But they also accept many other food types they encounter

The Agroecology of Carabid Beetles
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during their search that they can handle; these are eaten in lower amounts and may contribute more or less to beetle fitness ('supplementary food'). There is no absolute distinction between essential and supplementary food types, rather there exists a graded series of food qualities.

Methods for recording diets in the field

Interest in the feeding habits of carabid beetles has arisen from two main sources: 1) out of an interest in the carabid beetles themselves (what do they eat? how do they obtain their food? what is their role in the biological community?); and 2) out of an interest in the population dynamics of particular prey species (usually a pest). The methods used for studying carabid diets reflect this double purpose. They are described in detail elsewhere in this book (Symondson, this volume; Ingerson-Mahar, this volume); therefore only details pertaining to the recording of diet composition will be briefly mentioned here. Some methods are intended to record all sorts of food in the proportion eaten, though this is rarely achieved in full (e.g. microscopical analysis; iso-enzyme electrophoresis; serological or DNA analysis of gut contents). Others are aimed at recording all the different species that consume a certain food type (e.g. serological methods). Microscopical analysis of gut contents is only amenable for species that swallow the sclerotized parts of the prey (fragment feeders), while serological or molecular methods are needed for species with extra-oral digestion.

Feeding guilds

Thiele (1977) distinguished three feeding types based on the method of handling prey. These are equivalent to the groupings adopted by Forsythe (1982a, 1983) and Evans and Forsythe (1985): 1) fluid feeders with extra-oral digestion, 2) fragment feeders with no extra-oral digestion, and 3) mixed fluid and fragment feeders. Most species belong to the latter group. Thiele (1977) also classified carabids according to main food types into: polyphagous predators; oligophagous predators (mollusc, Collembola, and caterpillar specialists); and phytophagous carabids. The range of food types found in beetle stomachs includes both essential and supplementary foods. Since few studies of stomach contents make any attempt to quantify consumption rates, but rank prey by the proportion of beetles in which they are found, these studies tend to exaggerate the degree of polyphagy and underestimate the dependence on essential foods. Thus, based on stomach contents alone, Hengeveld (1980b) was able to distinguish only generalist and specialist feeders, the latter divided into Collembola and mollusc (snail and slug) feeders.

The following list of feeding guilds should not be viewed as a rigid classification system, because single species may comply to various degrees with more than one of the groups. Grouping stresses the differences between major adaptive forms but neglects variability within the groups. The feeding guilds have been recognized by combining several types of evidence: stomach contents, field and laboratory observations of feeding, and morphological analyses (e.g. structure of mouthparts and digestive tract). Physiological data on food utilization and food value are scant, as will be clear below, but are needed in order to precisely delimit the degree of feeding specialization of a species. The morphological variation has been documented

extensively by Forsythe (1982a, 1983), Evans and Forsythe (1985) and others, see Ingerson-Mahar (this volume). Data from many different sources indicate that feeding specializations are at least partly characteristic of tribes or even higher taxonomic levels (Hengeveld, 1981), suggesting that they have long evolutionary histories.

GENERALIST CARNIVORES

The vast majority of carabid beetles are generalist zoophages with different restrictions. They accept an extremely wide range of invertebrate prey, including earthworms, gastropods and arthropods, and they include plant material to various degrees (Lindroth, 1949/1992; Cornic, 1973; Luff, 1974; Sunderland, 1975; Sota, 1985). Scavenging is also common in this group. It has been recognized repeatedly that diet width of generalist carabids is correlated with the size of the animal (Loreau, 1983b; Pollet and Desender, 1987). For example, Tod (1973) noted that only large species included slugs in their diet. The extreme dietary width of *Pterostichus melanarius* was exemplified by Pollet and Desender (1985, 1986) who recorded 49 prey taxa at family level, including slugs, earthworms and a wide selection of insects. True broad-spectrum generalist carnivores are found among species of *Carabus*, *Abax*, large *Pterostichus*, and others (Thiele, 1977; Hengeveld, 1980b; Loreau, 1983a,b, 1994).

GENERALIST INSECTIVORES

Many smaller carabid species include slugs and worms to a very limited extent, but still accept a wide variety of insect prey, e.g. *Agonum dorsale*, *Trechus*, *Bembidion*, *Calathus*, amongst others (Davies, 1953; Mitchell, 1963; Zhavoronkova, 1969). They also include seeds and vegetation to only a minor degree, but scavenging on dead insects may be widespread. Even in *Cicindela* the proportion of dead insects may be 25% (Dreisig, 1981).

MOLLUSC SPECIALISTS

It has long been recognized that species of the tribe Cychrini prey predominantly on snails and slugs (Tod, 1973; Greene, 1975; Digweed, 1993) and show morphological adaptations to snail predation (Ingerson-Mahar, this volume). Several *Carabus* spp. have also been reported as predominantly mollusc feeders (Scherney, 1959, 1961), but most species of this genus also prey to a large extent on insects and thus may better be grouped as generalist zoophages. Predation by carabids on gastropods has been reviewed by Symondson (in press).

MICROARTHROPOD SPECIALISTS

Notiophilus spp., *Loricera pilicornis*, *Nebria brevicollis*, *Leistus ferrugineus* and others are known from stomach analyses to prey predominantly on Collembola and mites, whilst other soil-living arthropods serve as supplementary food (Davies, 1953; Anderson, 1972; Sunderland, 1975). Detailed studies of their morphology and prey-catching behaviour have revealed intricate adaptations to the capture of Collembola

with high escape abilities (Bauer, 1981; Hintzpeter and Bauer, 1986). Species of this group do not accept seeds or other plant material (Goldschmidt and Toft, 1997).

CATERPILLAR SPECIALISTS

Calosoma spp. prey predominantly on caterpillars of Lepidoptera and tenthredinid wasps and the literature contains little information on supplementary food types (cf. Larochelle, 1990). The relative monophagy of these species is confirmed by their populations fluctuating with caterpillar abundance (Weseloh, 1985).

GRANIVORES

Species of the genera *Harpalus* (s.lat.), *Amara*, *Zabrus*, *Synuchus*, *Ditomus*, and *Diachromus* are predominantly seed eaters. Their preference for seeds and supplementary feeding on insects has been documented both by stomach analyses (Skuhravy, 1959), laboratory experiments (Hagley *et al.*, 1982; Brandmayr, 1990; Jørgensen and Toft, 1997a,b) and observations (Schremmer, 1960; Trautner *et al.*, 1988).

OTHER SPECIALISTS

Family Carabidae worldwide contains several myrmecophiles and termitophiles, and other specialized habits are likely to be discovered. Some myrmecophiles seem to live predominantly with ants.

SUPPLEMENTARY FEEDING ACTIVITY

Scavenging on dead insects is no doubt a quantitatively important feeding mode for many carabids (Lindroth, 1949/1992; Dawson, 1965). Many carabids can be raised on meat but vertebrate scavenging is not likely to be of importance in nature. Carabids and staphylinids are often found in numbers at dead mammals or birds, but they may as well have been attracted because of the Diptera and other insects that gather at a corpse.

Herbivory other than granivory (consumption of plant leaves, fruits, pollen, fungi, etc.) is a common supplementary feeding mode as unspecified plant material is often found in gut dissections (e.g. Dawson, 1965). Apart from the true granivore beetles, inclusion of various plant materials in the diet of carabids seems to be supplementary feeding only (see below).

Larval feeding guilds

Carabid larvae seem to fit into the same feeding guilds as the adults. Though diet composition of carabid larvae rightfully is considered much neglected, all available evidence shows a close correspondence between larval and adult feeding habits. Broadly speaking, if the adult is a generalist, so is the larva; if the adult is a specialist, the larva has specialized on the same food type. The feeding techniques may differ, however. Carabid larvae are generally fluid feeders, including those that are fragment feeders as adults, e.g. *Nebria* (Spence and Sutcliffe, 1982).

In *Pterostichus madidus* both larvae and imagines are broad generalist insectivores, but whereas the imagines include plant material in their diet, the larvae do not (Luff, 1974). Schelvis and Siepel (1988) found that larvae of two *Pterostichus* spp. consumed a spectrum of small, soft-bodied invertebrates. Thus, soil-living insect larvae (Diptera, other Coleoptera), mites and earthworms formed the larger part of the diet, and cannibalism and mutual interspecific predation was substantial. These larvae must be characterized like the adults as generalist carnivores/insectivores; however, the exact menu is modified according to the smaller size, lower power and more edaphic life style of the larvae. According to Scherney (1961), three *Carabus* spp. larvae preferred earthworms and insect larvae, as eaten by the adults. Whereas the adults of *Abax parallelepipedus* eat a broad range of prey, the larvae could be mass reared without cannibalism on earthworms alone (Symondson, 1994).

Notiophilus and *Loricera* both have larvae specialized on Collembola, and they show morphological and behavioural adaptations to capture of Collembola which differ widely from those of the adults. Adult *Notiophilus* are diurnal hunters relying on good eyesight and high agility (Bauer, 1981); the larvae use mainly tactile cues to detect the same prey (Bauer, 1982). In *Loricera*, the adult beetles use their antennal setae to entrap Collembola (Hintzpeter and Bauer, 1986); the larvae use adhesive maxillary galea (Bauer and Kredler, 1988).

Larval Cychrini are snail specialists like the adults, though they do not have the characteristic body shape that is supposed to facilitate attack on snails by the adults (Greene, 1975).

Harpalus rufipes and *Amara similata* larvae were able to complete the full development on seeds alone (Luff, 1980; Jørgensen and Toft, 1997a,b), and are thus granivorous as the adults. *H. rufipes* was also able to develop on a pure insect diet, whereas *A. similata* was not. Thiele (1977) suggested that carabid larvae might be more specialized than the imago, though he recognized that extreme specialization had not evolved. Except for the effect of smaller size limiting the range of potential prey, there is little support for this suggestion (see also below).

Life style and foraging

Evans and Forsythe (1984) pointed out the different solutions to the trade-off between agility and powerfulness observed among the ground-living Carabidae. At one end of the spectrum are agile surface runners (e.g. *Cicindela*), at the other, soil-digging species (e.g. *Clivina*); in between are the larger proportion of species which push themselves through litter or vegetation. Arboreal climbers have adapted in other directions. All through this diversity of life style and habitat occupancy, being an opportunistic carnivore/insectivore is the basic feeding mode, though beetles will obviously encounter different types of prey and the exact diets will differ. Thus, the soil-digging *Clivina fossor* eats 'a variety of animal food' (Pollet and Desender, 1987): Collembola and soil-inhabiting invertebrates, such as insects, nematodes and enchytraeids. *Cicindela* takes 'mostly small insects': ants, beetles, spiders, Heteroptera nymphs, Collembola and Lepidoptera larvae (Dreisig, 1981). Arboreal *Dromius* eats 'softbodied insects and insect larvae' (Trautner, 1984).

If feeding modes are associated with a restricted habitat range, it is via the habitat distribution of the essential food. Thus, granivores are mainly searching for seeds on

the soil surface (Harpalini) or both on the surface and on low plants (Amarini). Slug feeders are also mostly restricted to near-surface layers. The caterpillar specialist *Calosoma sycophanta* climbs trees where caterpillars may occur in outbreak abundance.

Prey detection and attack behaviour

Wheater (1989) found good correspondence between feeding behaviour, type of prey and the senses used for prey detection in species of various feeding guilds. All species tested responded with attack when touching prey (tactile cues). Diurnal generalist insectivores (*Cicindela*, *Calosoma*, *Scarites*) used mainly vision, however, for detecting movable prey, while nocturnal generalist insectivores (*Pterostichus* spp.) used olfactory cues from prey, detected by the antennae. *Abax parallelepipedus* may be both day and night active and use both types of cues. *Cychrus* and two *Carabus* spp. (mollusc specialists) responded positively to contact with slug mucus, i.e. they probably used gustatory cues detected by the palps. Snail/slug specialists are thought to be able to follow mucus tracks.

In spite of their relatively narrow diet, the Collembola hunters use a variety of sensory modes for prey detection. *Notiophilus* have prominent eyes and are predominantly visual hunters (Bauer, 1981), but they also respond to gustatory cues from prey (Ernsting *et al.*, 1985). *Leistus* is a tactile hunter (Bauer, 1985), and Collembola specialist larvae seem to be the same (Bauer, 1982; Bauer and Kredler, 1988). One can hypothesize that the divergent strategies evolved to cope with Collembola are directed towards different types of Collembola, or to hunting in different microhabitats. Loreau (1983b) found *Leistus* preying predominantly on entomobryid Collembola, whereas *Notiophilus* preyed mostly on isotomids. Evolutionary constraints may also be involved: thus it may be difficult for larvae of holometabolous insects without composite eyes to evolve into efficient visual hunters.

Carabid responses to olfactory cues seem to be quite unspecific and do not necessarily indicate high food preference. In the studies of Kielty *et al.* (1996), the Collembola-specialist *Nebria brevicollis* was attracted to the odour of live Collembola. *Pterostichus melanarius* responded positively to live Collembola, live aphids and aphid alarm pheromone; however, in feeding tests, both Collembola and aphids were accepted in rather low amounts (Bilde and Toft, 1997b). Also, *Harpalus rufipes* responded to aphid alarm pheromone and wheat extract. This species is unable to utilize aphids (Jørgensen and Toft, 1997b) and is not phytophagous to any extent (Goldschmidt and Toft, 1997).

Daily and seasonal foraging cycles

Pollet and Desender (1986) demonstrated a coincidence of diel activity patterns of two species (*Loricera pilicornis*, *Bembidion properans*) and their most important prey groups as revealed by stomach analyses. However, this result tells little about possible adaptations of the beetles to secure an optimal diet. Diurnal beetles may take advantage of the possibility for basking in the sun, thereby achieving a high body temperature and agility that allow them to overpower otherwise difficult prey. Mitchell (1963) noted that *Bembidion lampros* stomachs were always empty outside

the warm season, whereas *Trechus quadristriatus* fed in all seasons. *B. lampros* is diurnal, with a high threshold temperature for feeding, 9°C (Mitchell, 1963; Sørensen, 1996). *Cicindela hybrida* has a lower feeding threshold at 20°C and a maximal capture rate at 35°C (Dreisig, 1981). Probably, diurnally and seasonally restricted activity are correlated. The feeding rate of *B. lampros* increased steeply at higher temperatures, compared to the nocturnal staphylinid *Tachyporus hypnorum* (Sørensen, 1995). Day-active species may thus be able to compensate for a short feeding time by a very high feeding rate at the optimal temperature.

A result of nocturnal activity may be that the carabid is predatorily active at a time when day-active prey (e.g. flies) are least active and least ready to escape an attack due to low temperature. P.D. Kruse (unpublished) found in the laboratory that *Calathus fuscipes* were able to catch more fruit flies at 5°C than at higher temperatures. This effect was apparent only in darkness; under light conditions, the nocturnal beetles were inactive. Flies may often be high-quality prey (see below), so adaptations that secure a higher proportion of flies in the diet may have great fitness value. A whole category of prey (flying insects) may be more available to less agile predators at the time of the day (or during the seasons) when they are least active.

Seasonal variation in diets has been demonstrated in most extensive studies of stomach contents, primarily reflecting fluctuations in availability (Dawson, 1965; Koehler, 1976; Loreau, 1983a; Lukasiewicz, 1996). Skuhravý (1959) found *Poecilus cupreus* to take mainly plant material early in the season and insect food during summer. Cornic (1973) found the same pattern in *Harpalus affinis* and *H. rufipes*. Since *Pterostichus* and *Harpalus* have opposite preferences regarding insect and plant (seed) food, there is no logical pattern, indicating again that they are opportunistic feeders.

Diet quality

So far, we have considered the diets of carabid beetles from the information that can be obtained from simply recording what they eat. However, a full evaluation of stomach contents can only be obtained if we know the nutritional value of each type of food for the carabid species and how the food types in the menu interact to determine the value of the complete diet. Studies taking this approach are still rather few. Comparative data are available only for species from some of the feeding guilds and for just a few food types.

Food contains four basic constituents: energy, nutrients, toxins and indigestibles. The value (or quality) of a diet or a type of food may depend on the proportion of each of these constituents. But it cannot be evaluated by measuring them, e.g. in a chemical analysis. The same type of food may be high quality to one species and of no value to another, depending on the physiological demands (specializations) of the consumer. Therefore, diet/food value is best defined by its potential contribution to the fitness of the consumer. This definition implies that the value of a food type may vary with the developmental phases of the consumer and depend on what other food it has eaten. This is not a weakness, merely a reflection of the complexity of food quality.

In practice, food value is measured by comparing the performance of individuals when the food type is added to the diet compared to the same diet without the food type. In the simplest case, the comparison is between individuals given one food type

and starved controls. Such experiments are especially relevant when the food type is of low quality: if performance is reduced in a diet treatment compared to a starvation treatment, this indicates the presence of a toxic substance (cf. Toft and Wise, 1999a). More often, the comparisons are between diets with various numbers of elements, e.g. between differently mixed diets or mixed vs. monotypic diets. Evaluation of a food type should preferably include several comparisons, e.g. monotypic diet of test food vs. monotypic diet of known high-quality food type ('comparison food'); comparison food vs. mixed diet of comparison + test foods; same mixed diet with vs. without test food, etc. To our knowledge, there are still no experiments analysing the contribution of a food type to the value of a naturally mixed diet. Logistic constraints will usually prevent such experiments since natural diets may be very diverse. *A priori* one would expect the importance of single food types to decrease the more varied the total diet, so that any single element may be deleted without negative effects. However, in no case of a highly polyphagous species have we any idea of how many of the dietary elements are high quality (essential) and how many are low quality (supplementary) food types, or even if carabids are capable of detecting such differences prior to feeding.

Fitness related life-history parameters can function as indicators of diet quality (Toft, 1996). Total life-cycle fitness is not necessarily the best experimental choice because dietary demands may change during ontogeny and several gradations below zero total fitness are possible. For example, we would assign a higher value to a food type that allows a species to develop through one or two larval instars than to a food type on which the larvae die in the first instar. The life-history parameters most commonly used as quality criteria are (larval) survival, rate of development, growth rate, teneral size, longevity of imagines, and female fecundity (examples below).

A relative and partly subjective classification of food/diet quality proposed by Toft and Wise (1999a,b) will also be used in the following. 'High quality' food allows high (maximal) survival, growth rate, fecundity, etc.; 'intermediate quality' food allows submaximal performance; 'low quality' food sustains performance above zero and may contribute positively to a mixed diet; 'poor quality' food is no better than starvation or makes no improvement in a mixed diet; 'toxic' food leads to a performance below that of starved beetles (e.g. higher mortality) or reduces the value of a mixed diet. The quality assignments may result from the balance between positive effects of nutrients and negative effects of toxins and deterrents (and other factors, e.g. a hard exoskeleton). Thus, food of all quality categories may contain deterrents or toxins, probably in increasing relative amounts from high-quality to toxic foods.

Food utilization indices (Waldbauer, 1968) or equivalent co-variance analysis (Raubenheimer and Simpson, 1992; Horton and Redak, 1993) provide information about how quality is achieved, rather than indicate quality as such. If food is deterrent, low consumption rates will result in low overall quality, even if utilization efficiency is high. Food containing a toxin will usually be consumed at low rates and utilization efficiency will also be low. Food without toxins or deterrents, but of poor nutrient composition, is expected to be eaten at high rates, but with low utilization efficiency (Toft, 1996).

Considering the diversity of the diets of different species (and probably individuals), an interesting question is to what extent feeding specializations are reflected as differences in food value. Have feeding guilds evolved mainly as morphological/

behavioural (i.e. life style) adaptations that make some species more likely to encounter and acquire certain types of food/prey, which therefore make up the larger part of the diet, with no differentiation in food value? Or do these feeding specializations also have physiological/biochemical counterparts that differentially define specific essential and supplementary food types for species of different feeding guilds, or even within feeding guilds?

Value of different types of food

It can be assumed that prey types to which carabid species show specific adaptations are also high quality prey for these beetles, e.g. snails to snail specialists, Collembola to Collembola specialists, etc. The truth may not necessarily be as simple as that, however. Within each prey group, species are differently adapted to defend themselves against their predators. Thus, Digweed (1993) found varied preference of the cychrine *Scaphinotus marginatus* for different species of snails and slugs. He suggested this might be due either to differences in nutritional value or to anti-predatory defences (mucus production, shell thickness, etc.). Since food value cannot be judged from preference or consumption rate studies but only from performance experiments, the following paragraphs will deal mainly with food types for which performance results are available. *Table 3.1* summarizes the data known to us from such studies with natural prey or seeds, i.e. neglecting 'laboratory prey' like mealworms, fruit flies, etc. Included are also the results concerning the value of specific food types in mixed diets.

APHIDS

The incentive for much of the work on feeding habits of carabid beetles in agricultural habitats originated from an interest in the potential of these predators for limiting aphid populations in crops, in particular cereal fields (see Sunderland, this volume). The value of the aphids themselves is therefore of special relevance. Bilde and Toft (1994) found a low preference in *Agonum dorsale* for the cereal aphid *Rhopalosiphum padi* relative to the comparison food, *Drosophila melanogaster*. In accordance with this, the consumption capacity for the aphid was much lower than for the fruit fly, and this was the case whether tested with pure diets or a mixed diet. Even if the beetles were starved for seven days, the consumption capacity remained at the same low level. This result probably implies that the aphid consumption rate is limited by a low tolerance of the beetle to a chemical in the aphid that consequently serves as an anti-predator defence. The egg-laying rate of females kept on a pure aphid diet was much reduced, probably a composite effect of low feeding rate and low utilization efficiency. A deterrent effect of the aphid was demonstrated by Bilde and Toft (1994) by coating palatable fruit flies with aphid homogenate: *Agonum dorsale* showed a significantly lower preference for the coated flies compared to uncoated flies. So far, the presumed chemical defence of the cereal aphids has not been identified, and it is unknown whether it originates from the host plant or is synthesized by the aphids.

Bilde and Toft (1997a,b) extended the observation that aphids are of low palatability to several carabid species, and this applied partly to two additional species of cereal aphids. Capacity for aphid consumption did not exceed that for fruit fly

Table 3.1. Summary of studies determining the food value of natural insect prey or seeds [and their contribution to mixed diets] to carabid beetles. Relative value categories: High – Intermediate – Low – Poor – Toxic (defined in text).

Food/prey type	[Mixed with]	Carabid species/instar	Fitness parameter	Value	[Mixing effect]	Ref.
Seeds						
Mixed seeds 9 spp.		*Amara similata*	Fecundity	High		6
Mixed seeds 9 spp.		*Amara similata* larvae	Survival	Interm.–High		6
Mixed seeds 8 spp.		*Harpalus rufipes*	Fecundity	High		7
Mixed seeds 7 spp.		*Harpalus rufipes* larvae	Survival	Interm.		7
Poa annua		*Amara similata*	Fecundity	Low		6
Poa annua		*Amara similata* larvae I	Survival	Low		6
Poa annua		*Harpalus rufipes* larvae	Survival	High		7
Taraxacum sp.		*Amara similata*	Fecundity	Interm.		6
Taraxacum sp.		*Amara similata* larvae I larvae II–III	Survival	Low High		6
Taraxacum sp.		*Harpalus honestus* larvae	Developmental rate	High		4
Tripleurospermum inodorum		*Amara similata*	Fecundity	Interm.		6
Tripleurospermum inodorum		*Amara similata* larvae	Survival	Low		6
Tripleurospermum inodorum		*Harpalus rufipes* larvae	Survival	Interm.–High		7
Capsella bursa-pastoris		*Amara similata* larvae	Survival	High		6
Papaver rhoeas		*Amara similata* larvae	Survival	Interm.		6
Trifolium repens		*Amara similata* larvae	Survival	Low		6
Trifolium repens		*Harpalus rufipes* larvae	Survival	Interm.		7
Daucus/Umbelliferae		*Harpalus honestus* larvae	Developmental rate	High		4
Umbelliferae		*Ophonus ardosiacus* larvae	Survival	High		4
Gastropods						
Tandonia budapestensis		*Pterostichus melanarius*	Survival	Toxic		10
Earthworms						
2 spp.		*Abax parallelepipedus* larvae	Survival, growth rate	High (no comparisons)		9
Lumbricus terrestris		*Agonum dorsale*	Fecundity	Poor–Low		2
Insects						
Mixed insects 4 spp.	[Mixed seeds]	*Amara similata*	Fecundity	Low	[No]	6
Mixed insects 3spp.	[Mixed seeds]	*Amara similata* larvae	Survival	Low	[No]	6
Mixed insects 3 spp.	[Mixed seeds]	*Harpalus rufipes*	Fecundity	Low	[No]	7
Mixed insects 3 spp.	[Mixed seeds]	*Harpalus rufipes* larvae	Survival	Low	[No]	7
Lepidoptera						
Lymantria dispar larvae		*Calosoma sycophanta*	Fecundity	High		12

Aphids						
Rhopalosiphum padi	[*Poa annua* seeds]	*Amara similata*	Fecundity	Poor–Low	[No]	6
Rhopalosiphum padi		*Calathus melanocephalus*	Fecundity	Low		3
Rhopalosiphum padi	[Cat food]	*Poecilus cupreus*	Fecundity, egg size	High?	[No]	11
Rhopalosiphum padi	[Cat food]	*Bembidion lampros*	Fecundity, egg size	Interm.	[Pos.]	11
Rhopalosiphum padi	[Cat food]	*Pterostichus melanarius*	Fecundity, egg size	Low–Interm.	[No]	11
Rhopalosiphum padi		*Agonum dorsale*	Fecundity	Low		2
Rhopalosiphum padi		*Amara similata* larvae	Survival	Poor		6
Rhopalosiphum padi		*Harpalus rufipes* larvae	Survival	Low		7
Rhopalosiphum padi		*Bembidion lampros* larvae	Survival	Interm.		8
Sitobion avenae	[*Capsella bursa-pastoris* seeds]	*Amara similata* larvae	Survival	Poor	[No]	6
Sitobion avenae		*Calathus melanocephalus*	Fecundity	Low		3
Sitobion avenae		*Bembidion lampros* larvae	Survival	Interm.		8
Metopolophium dirhodum		*Amara similata*	Fecundity	Low		6
Metopolophium dirhodum		*Calathus melanocephalus*	Fecundity	Low		3
Metopolophium dirhodum		*Amara similata* larvae	Survival	Poor		6
Metopolophium dirhodum		*Bembidion lampros* larvae	Survival	Interm.		8
R.padi+S.avenae+M.dirhodum-mix		*Calathus melanocephalus*	Fecundity	Low		3
Collembola						
Orchesella cincta		*Notiophilus biguttatus*	Fecundity	High (no comparisons)		5
Orchesella cincta		*Notiophilus biguttatus* larvae	Growth rate, survival, adult size	High (no comparisons)		5
Isotoma anglicana		*Bembidion lampros*	Fecundity	Low–Interm.		1
Isotoma anglicana		*Bembidion lampros* larvae	Survival, development, adult size	Interm.–High		1
Isotoma notabilis		*Bembidion lampros*	Fecundity	Poor		1
Isotoma notabilis		*Bembidion lampros* larvae	Survival, development, adult size	Low–Interm.		1
Isotomurus prasinus		*Bembidion lampros*	Fecundity	Low–Interm.		1
Folsomia fimetaria		*Bembidion lampros*	Fecundity	Low–Interm.		1
Folsomia fimetaria		*Bembidion lampros* larvae	Survival, development, adult size	Interm.–High		1
Lepidocyrtus cyaneus		*Bembidion lampros*	Fecundity	Low–Interm.		1
Mixed animal diets						
Rhopalosiphum padi+Lumbricus terrestris+Drosophila melanogaster		*Agonum dorsale*	Fecundity	High		2

Refs.: 1 – Bilde *et al.*, 2000; 2 – Bilde and Toft, 1994; 3 – Bilde and Toft, 1999; 4 – Brandmayr, 1990; 5 – Ernsting *et al.*, 1992; 6 – Jørgensen and Toft, 1997a; 7 – Jørgensen and Toft, 1997b; 8 – Sørensen, 1996; 9 – Symondson, 1994; 10 – Symondson, 1997; 11 – Wallin *et al.*, 1992; 12 – Weseloh, 1993.

consumption in any species studied, and was frequently significantly lower. In most species, capacity for consumption of *R. padi* was lower than for *Sitobion avenae*, which was again lower than for *Metopolophium dirhodum*. Consumption capacity for the latter species was generally not different from that of fruit flies. The background for the different palatabilities of these aphids is unknown. Consumption rates of the three cereal aphids by *Bembidion lampros* were also low (Sørensen, 1996). However, *B. lampros* larvae were able to develop through all instars to adult stage on single-species diets of the three aphids, and thus seem to be more tolerant to aphids than are the adults (Sørensen, 1996). Still, the larval developmental time and the weight of the teneral adults ranked the three aphids species in the same order as found for consumption rates of other predators. One species, *Calathus melanocephalus*, showed a consumption capacity of *R. padi* as high as that for fruit flies (Bilde and Toft, 1997b). Bilde and Toft (1999) tested the hypothesis that a high tolerance to this prey would indicate a better ability, compared to other carabid species, to utilize aphids for maintaining performance. This was not the case. Single-species diets of the three cereal aphids (as above) and the 3-species mixed diet all resulted in similarly decreasing fecundity rates, indicating depletion of resources for egg laying. Control beetles held on fruit flies maintained a high egg-laying rate. Thus, tolerance to consumption of these prey showed no correspondence to their food value, neither between aphid species nor between aphids and fruit flies.

The evidence for aphids as low quality prey for carabid beetles is all based on laboratory studies in which the diets of individual beetles can be controlled. Supporting evidence from the field can be obtained indirectly by testing predictions based on the low-quality assumption. Pollet and Desender (1988) found by stomach dissections of 12 common carabid beetles that each stomach contained only one, or very few, aphids. Collembola, on the other hand, were often found in multiples in the same species. This is the predicted pattern if aphids are low-quality prey and Collembola are high-quality prey forming the bulk of the biomass consumed (see below).

Another prediction is that carabids should aggregate where there are high densities of their preferred food, but not at high densities of aphids or other low-quality prey. In seeming contradiction of this, Bryan and Wratten (1984) demonstrated in field experiments that several carabids aggregated with aphids. The aphid densities created in this study were exceptionally high. However, Monsrud and Toft (1999) hypothesized that potential high-quality prey insects would be more abundant at aphid colonies because they were attracted to honeydew secreted by the aphids. They found a significant attraction of Diptera and several species of carabid beetles to plots where honey was sprayed, compared to plots with augmented aphid numbers, as predicted. Interestingly, they found significant aggregation of carabid and staphylinid larvae where aphid numbers had been augmented. This would be expected if aphids can be better utilized by the larvae, as indicated above. However, most larvae are relatively immobile, whereas aphid populations show considerable spatial fluctuation (Winder *et al.*, 1999). The spatial response of carabids to cereal aphids is currently investigated using naturally occurring populations (J.M. Holland, pers. comm.).

Since aphids are supplementary food that cannot usually be consumed in high quantities by individual beetles, and that cannot alone support carabid populations, the densities of carabid populations, and consequently their potential impact on aphid populations, depend on the presence of high-quality alternative prey.

COLLEMBOLA

Together with Diptera, springtails may be an important group of prey supporting carabid beetle populations, at least as regards small- to medium-sized species. They occur in most ecosystems in very high numbers and often with many species adapted to different microhabitats (Hopkin, 1997). Some are agile surface-active species with a powerful furca and a good jumping ability. Others live in the soil spaces, have reduced or no furca, and rely on chemical defences against their predators. Toxic or deterrent compounds have recently been identified from species of several families (Dettner *et al.*, 1996; Messer and Dettner, 1997; Messer *et al.*, 2000) and further behavioural evidence was reviewed by Messer *et al.* (2000). It is therefore highly relevant to ask if carabids accept Collembola indiscriminately, or whether some types of Collembola are more important than others. Very few studies have been published that specifically compare the value of Collembolan species to a carabid.

Bilde *et al.* (2000) measured the egg-laying rate of *Bembidion lampros* held on single-species diets of five Collembola species, compared to fruit flies *D. melanogaster*. Four of the species were Isotomidae and one an Entomobryidae. All Collembola species turned out to be lower quality food to *B. lampros* than fruit flies. Comparing the feeding rates and the efficiency of prey utilization created a complex pattern, indicating a diversity of mechanisms were responsible for the predator–prey interactions. Some species were eaten in only low amounts, but the efficiency of transforming food into eggs was high; such species probably have strong feeding deterrents, but a good nutrient composition and no toxins. Others were eaten in rather large amounts, though fecundity was low, indicating either poor nutrient composition or the presence of a weak toxin. One species was eaten to only a very small extent, but this stopped egg production completely. Only on fruit flies were both consumption rate and conversion efficiency high. Selecting the right kind of Collembola for food may thus have strong influence on beetle fitness.

Bilde *et al.* (2000) also analysed the value of three of the Collembola species and fruit flies to *B. lampros* larvae by raising them on single-species diets. Though differences in quality were found, and fruit flies were again of highest quality, all three Collembola species (including the one that stopped egg production) allowed complete development to adult beetles of at least some individuals. This indicates that the larvae may be better adapted to cope with the presumed chemical defences of these Collembola than are the adults. It is tempting to speculate that carabid larvae may be closer coevolved with the soil-living microarthropods.

The intermediate value of the tested Collembola species to *B. lampros* is probably not fully representative of the role of Collembola to carabid beetles. First, several species have evolved as Collembola specialists. Thus, at least some springtail species are likely to be high-quality food to them (cf. Ernsting *et al.*, 1992), but studies comparing with other prey types are not available. *Loricera pilicornis* showed a higher consumption rate of *Isotoma anglicana* than of fruit flies and aphids (Bilde and Toft, 1997b). This springtail was also tested with *B. lampros* (Bilde *et al.*, 2000). It is possible that it is a high quality prey to the Collembolan specialist, but intermediate quality to generalist *B. lampros*. Collembola species of the same genus or family may differ widely in quality as food for the same predator (Toft and Wise, 1999a; Bilde *et al.*, 2000).

DIPTERA

Adult Diptera are persistently recorded at high frequencies in stomach dissection studies of generalist insectivores (Sunderland, 1975; Hengeveld, 1980a,b; Pollet and Desender, 1985, 1987, 1989). This is one argument for our use of *D. melanogaster* (fruit fly) as standard comparison food of high quality in our studies. With very few exceptions, fruit flies have turned out as the top quality food in tests with generalist insectivores (Bilde and Toft, 1994, 1997a,b, 1999). Drosophilids are also common in most kinds of habitats, including agricultural fields, and they were recorded as food for *P. melanarius* by Pollet and Desender (1985). Unfortunately, the value of other Diptera, as well as Diptera larvae and pupae, has not been systematically studied.

Sciarid midges: specific mention of Sciaridae as carabid prey is given by Pollet and Desender (1985). Larvae of sciarid midges are abundant in most types of soils and may be an important food source for small carabid larvae and small adults. Sciarid midges are low-quality food for wolf spiders (Toft and Wise, 1999a) and the available evidence indicates that the same may be true for carabids. Thus, *A. dorsale* showed a low preference for fruit flies coated with homogenate of adult sciarids compared to uncoated flies (Bilde and Toft, 1994).

LEPIDOPTERA

Calosoma sycophanta can sustain a high reproductive rate on a monotypic gypsy moth caterpillar diet (Weseloh, 1993). Most probably, this species, and larvae and pupae of several other species of moths and sawflies, are good carabid food. Large carabids thus contribute substantially to the density-dependent pupal mortality of winter moths (cf. den Boer, 1986). Greater wax moth larvae, however, were poorly utilized by *C. sycophanta* (Spieles and Horn, 1998).

DIPLOPODS

Snider (1984) found in laboratory experiments that five species of *Pterostichus* consumed large numbers of diplopods, in spite of the defensive secretions of these animals. The sizes taken depended on the size of the beetles. *Pterostichus* larvae ate large numbers of young instar diplopods. As a *Staphylinus* sp. was able to develop from hatching to imago on a sole diplopod diet, it is suggested that the carabids might do the same.

SEEDS

It is now well established that species of Harpalini, Amarini, Zabrini, Ditomini a.o. rely on seeds as their main food source (Schremmer, 1960; Thiele, 1977; Luff, 1980). For at least some species of *Harpalus* and *Amara* this holds true for both the adults and the larvae (Brandmayer, 1990; Jørgensen and Toft, 1997 a,b). Different seeds vary in food quality to these seed specialists; however, Jørgensen and Toft (1997a) found no correspondence in seed quality between adults and larvae. This may be because quality is determined mainly by seed size and hardness rather than nutritional composition; some highly nutritious seeds may be inaccessible to the small larvae.

The evolution of granivory from carnivory is understandable given the often high concentration of protein and lipids found in seeds as in carnivore food (Slansky and Panizzi, 1986).

Seeds are accepted also by species of generalist feeding guilds, e.g. *Carabus*, *Bembidion*, *Trechus*, *Calathus* and *Pterostichus* (Goldschmidt and Toft, 1997). The amounts of seed eaten by these species were much below that of *Harpalus rufipes*, even if no better food was available. This indicates a limited ability to utilize seed in the generalist carnivores and insectivores, but nothing is known about the nutritional value of seed to these carabids. Specialist Collembola feeders (*Loricera*, *Notiophilus*) did not accept seeds. Consumption of seeds by Carabidae is discussed further in Tooley and Brust (this volume).

PLANT MATERIAL

Unspecified plant material is often listed in stomach dissection studies. Dawson (1965) distinguished fragments of higher plants, pollen, fungal hyphae and spores, and diatoms. From an ecological point of view, distinction is important, partly because of the great differences in nutrient content, partly because granivory, phytopagy and detritivory have very different impacts in the ecosystem. According to Thiele (1977), *Zabrus* 'eats young leaves of the newly sprouting winter crop', and Luka *et al.* (1998) report herbivory on rape plants (young fruits, stems, flowers) by *Amara* spp., but to a limited extent. No laboratory study has evaluated green plant material, detritus or fungi as food for carabids. Goldschmidt and Toft (1997) compared the preferences of 25 species for seeds and pieces of fresh wheat leaf. Phytophagy (consumption of green leaves) occurred in most insectivorous species (except some Collembola specialists and a few of the generalist insectivores); quantitatively, phytophagy occurred in these species at a lower or same level as granivory. In the granivore *Harpalus rufipes*, phytophagy was recorded, but in even lower frequency than in the insectivores. Brandmayr (1990) suggested that consumption of leaves and fruits by carabid beetles served only to obtain water. Sota (1984) compared the effects of minced beef and various fruits on performance of *Leptocarabus kumagaii*. On the fruit diet, oviposition ceased and the females lost weight, but they stayed alive for the one-month observation period. Also, the males were able to stay alive for a long time on the fruit diet. According to Weseloh (1993), *Calosoma sycophanta* females cease egg laying if fed only grapes. Sota (1984) concluded that acceptance of plant food might enhance survival under food limited conditions.

Phytophagy, detritivory and fructivory thus occur in many carabid species as supplementary feeding activity. Their nutritional importance for growth and reproduction is probably low.

SNAILS AND SLUGS

The fact that some carabids have specialized as snail and slug feeders in both larval and adult stages would indicate a high food quality of these prey. Other large generalist carnivore species (e.g. *Carabus* spp., *Abax parallelepipedus*, *Pterostichus melanarius*) have been found to readily accept slugs and snails (Scherney, 1959, 1961; Loreau, 1983a,b; Symondson, 1994). Symondson (1993) and Symondson *et al.*

(1996) also found evidence that slugs were preferred prey for the two latter species, and Symondson *et al.* (1996) and Bohan *et al.* (2000) presented evidence for important predation on slugs. Their results indicate preferential feeding and aggregation at high slug densities. This is only indirect and unreliable evidence of a high food quality of slugs, and slugs may become abundant without a concomitant increase of large carabids. The relative food value of slugs to various generalist carnivore and insectivore carabids thus needs more detailed study. If slugs are only mediocre food, the control efficiency of the large carabids will depend on presence of high-quality alternative prey.

One species of slug was found to be toxic to *Pterostichus melanarius* that may die within a few days after eating it (Symondson, 1997). Production of mucus by slugs may reduce or prevent predation by many carabids (Symondson, in press). Little seems to be known about predation on gastropod eggs, which are often highly vulnerable to predation from carabids. In several species, the eggs contain defensive chemicals (Symondson, in press).

EARTHWORMS

Earthworms are assumed to be high-quality food for some species of the generalist carnivore guild because they are frequently found in stomach analyses, and some species have been bred on earthworms (Symondson, 1994, and references therein). Mass rearing of *Abax parallelepipedus* larvae on a sole diet of earthworms without cannibalism is evidence of nutritional sufficiency of this prey. Symondson *et al.* (2000) found that *P. melanarius* consumed more earthworms when other prey were scarce, indicating that earthworms are only acceptable but non-preferred food. Comparative performance studies are lacking, however, for these species. Earthworms were low-quality food for two species of generalist insectivores, e.g. with respect to larval growth and survival in *P. nigrita* (Ferenz, 1973, cited after Thiele, 1977), and with respect to fecundity in *Agonum dorsale* (Bilde and Toft, 1994).

OTHER PREY GROUPS

Some prey groups may be widespread supplementary food or essential food for local populations or single species. Isopods may be extremely abundant in many habitats. In spite of this, carabid predation seems to be limited (Sunderland and Sutton, 1980). By contrast, talitrid Crustacea are claimed to be the chief dietary constituent of the seaside-living *Eurynebria complanata* (King and Stabins, 1971). Where they are abundant, terrestrial caddis fly larvae may be important prey for *Pterostichus oblongopunctatus* (den Boer, 1986). Comparative studies on the food value of these prey are lacking.

Food quality in relation to dietary guilds

Several papers give simple recipes on how to raise carabid beetles in the laboratory. Thus, Goulet (1976) claimed to have bred 80 species, including representatives from all the above listed feeding guilds, with mealworms as the only food. Thiele (1977) used mealworms, minced beef or dog biscuits, while Burakowski (1986) used ant

larvae and pupae. This ability to subsist on what must be regarded 'atypical' food for several of the species involved underlines the earlier statement that carabid feeding specializations are only partial. The exact degree of specialization (i.e. relative ability to utilize the main potential food types for improved fitness) has still not been elucidated for any species. Only scattered pieces of the puzzle are available.

In the insectivore *Agonum dorsale*, Bilde and Toft (1994) found a higher fecundity when fed *D. melanogaster*, compared to earthworms. Unfortunately, no similar study seems to exist for an earthworm or a slug specialist. Two generalist carnivores (*Pterostichus madidus* and *Abax parallelepipedus*) showed different slug antigen decay rates in the crop in spite of no difference in the rate with which slug food was processed through the crop (Symondson and Liddell, 1993). This may indicate a different ability to digest slug protein and thus possibly reflect a different degree of adaptation to slug predation.

The most extensive comparative information is available on species of the granivorous guild. Cornic (1973) reported a higher proportional intake of insect food during reproductive periods in *Harpalus affinis* and *H. rufipes*, suggesting a nutritional benefit of insectivory for egg development. These results were not confirmed in the laboratory tests of Jørgensen and Toft (1997a,b), who found substantially higher fecundity in *Amara similata* and *H. rufipes* on mixed-seed diets than on mixed-insect diets. In none of the species did the combined diet of mixed seeds + mixed insects improve fecundity, compared to the reference diets. Thus, insects as supplementary food were of no value. Allen and Hagley (1982) were able to detect antigen from Lepidoptera larvae longer in both *Harpalus affinis* and *Amara* sp. than in *P. melanarius*, indicating a slower digestion rate of insect material in the granivorous than in the insectivorous species. Larvae of *A. similata* were even more dependent on seeds than the adults since they were unable to reach maturity on an insect diet (Jørgensen and Toft, 1997a). *H. rufipes* larvae, on the other hand, were better able to utilize insects for development; seeds, insects, and the combined diet gave the same success (Jørgensen and Toft, 1997b).

In conclusion, though the value of supplementary foods may vary between species of the same feeding guild, the scattered evidence supports the notion that supplementary foods are usually of lower quality than essential foods. This may not sound very surprising. However, it may help to resolve the conflict between the seemingly specialized mouthpart morphology of many species (see Ingerson-Mahar, this volume) and their 'opportunistic polyphagy', as indicated by stomach dissections. The food quality data support the conclusion of limited polyphagy, as do the morphological evidence.

As supplementary food types may sometimes turn out to have very low nutritional value as measured in fitness tests, the question arises as to why they are so often recorded in stomach contents. A good example is the consumption of aphids in cereal fields. Sunderland *et al.* (1987) found aphids in the stomachs of 81 taxa of generalist predators, but probably they are low-quality food to all of them (cf. Bilde and Toft, 1994, 1997a,b, 1999, 2000; Toft, 1995). Ease of capture, and the need to learn (if possible) the nutritional value or deterrence of a prey type in order to reject it, may be one explanation. Another possible answer may be that supplementary foods are of sufficient value to keep the beetles alive, even if insufficient for active growth and reproduction. Acceptance may thus have survival value, especially in periods of food

scarcity. Extended survival on a pure aphid diet was found in nymphs of a linyphiid spider, though the aphid contributed nothing to growth (Toft, 1995). Another possibility is that the aphids in some dietary combinations do contribute significantly to predator fitness and therefore are not generally rejected (Bilde and Toft, 1994). Bilde and Toft (2000) found some evidence in a spider that aphid consumption improved fitness if the remaining diet was of relatively low nutrient quality, but not if it was high quality.

Physiological and biochemical correlates of dietary specialization

The digestive system of carabid beetles comprises all the main types of digestive enzymes, including proteases, lipase/esterases, chitinase, cellulase, amylase, laminarinase, and oligosaccharidases (Forsythe, 1982b; Jaspar-Versali and Jeuniaux, 1987; Jaspar-Versali *et al.*, 1987; Terra *et al.*, 1996). Both fluid and mixed feeders regurgitate mid-gut enzymes for initial pre-oral digestion. In all carabids, the main digestive activity is concentrated in the crop, though again accomplished by mid-gut secretions. Terra *et al.* (1996) concluded that insect digestive enzymes are quite similar, in spite of differences in diet composition, since 'most species possess the full array of hydrolases'. This generalization may be true at a superior level, but should possibly be modified in the details. Vaje *et al.* (1984) found high intra- and especially inter-specific variation in proteases in *Carabus* spp., though the functional significance of this diversity is unknown. Jaspar-Versali and Jeuniaux (1987) demonstrated differences in the activity of several digestive enzymes among species of different feeding guilds. They found much higher cellulase activity in *Abax parallelepipedus* and *P. melanarius* (both feeding frequently on vegetable matter) than in five more strictly carnivorous *Carabus* spp. These results are suggestive of a fitness-enhancing effect of vegetable consumption in some species which still has to be demonstrated. *Carabus*, on the other hand, had higher levels of protease activity. The two groups showed equal chitinase activity; for both, insects form an important part of the diet. A similar study including granivore species would be highly welcome.

Food preferences

Food preferences as they are measured in standard laboratory experiments, are always a composite phenomenon, reflecting factors relating to discovery of the prey (activity), ease of capture (e.g. size, escape ability), ease of handling (e.g. size, hardness), and food value (e.g. palatability, nutrient content) (Mitchell, 1963; Pollet and Desender, 1986; Bilde and Toft, 1994). Wheater (1988) found a positive correlation between gape distance of carabid species and median prey size. Pearson and Mury (1979) found similar relationships in tiger beetles. Hardness imposes costs of handling, but heavily sclerotized prey also wears the mandibles more than soft prey, with possible negative consequences for foraging efficiency and reproduction (Houston, 1981; Wallin, 1988). The same may be true for seeds. Hard seeds may pose mechanical difficulties for small larvae of granivore species and thus be out of the list of potential food, in spite of being high-quality food for larger larvae (Jørgensen and Toft, 1997a).

Pollet and Desender (1987) found that predation on several insect groups was

positively correlated with prey density, but negatively correlated with prey activity. Ernsting and Jansen (1978) showed how prey mobility is important for the visual hunter *Notiophilus biguttatus*. A particularly instructive experiment was performed by Lang and Gsödl (2001), who compared the preferences of *Poecilus cupreus* for crickets, *Drosophila* and the cereal aphid *Rhopalosiphum padi*, when these prey were offered live and dead, respectively. When prey was offered alive, the order of preference was aphid > *Drosophila* > cricket. When offered dead, preferences were reversed. Obviously, with dead prey, the beetles selected according to food value, while ease of capture determined preference order of live prey. This may also explain the findings of Kielty *et al.* (1999), who found preference of *P. cupreus* and *P. melanarius* for cereal aphids over entomobryid Collembola in live prey experiments.

Carabid beetles of all feeding guilds prefer highly nutritious foods: animal matter or seeds. However, the requirements for specific nutrients have not been determined (Lövei and Sunderland, 1996). R. Wedfeldt and M. Kirkegaard (unpublished) used completely artificial agar-based diets to test for ability to select food with different protein:carbohydrate ratios (80:20 or 20:80). They found non-random selection for the high-protein food in two species, *Agonum dorsale* and *P. melanarius*.

Hengeveld (1980a) discussed food specializations in Carabidae, stating that 'a specialist is not simply a species with fewer diet components, but one that selects its prey'. Given the dramatic differences in quality of different potential prey types and the different consumption rates of various prey, it is clear that all carabids must show some degree of selectivity. We prefer to think of specialist and generalists as animals that select before and after capture, respectively. Specialists probably respond to a more restricted range of cues (may have an innate 'search image') characteristic of their preferred food. Generalists initially accept a very wide range of foods but become more selective as a result of experience. This increased selectivity is most likely to be based on the development of aversions to low-quality food (cf. Toft, 1997; Toft and Wise, 1999a,b). The different mechanisms of selectivity will result in a wider prey spectrum for the generalists because they need to test all potential prey types before they become selective.

Acquired aversions may develop to sub-optimal prey whether the inferiority is due to skewed nutrient balance or chemical defences (Bernays, 1993), but are not always a safeguard against toxin consumption. Herbivores or detritivores with chemical defences may have sequestered the toxin from their own food. These toxins in turn reduce the food value of the prey to their predators. In extreme cases, this may have detrimental effects on populations of carabid beetles. Den Boer (1986) described how the fecundity of *Calathus melanocephalus* was reduced during outbreaks of the heather beetle (a chrysomelid beetle). The carabid population fluctuated in a delayed density-dependent manner. Presumably, when the toxin containing larvae of the heather beetle became very numerous, the carabids ate more than they could tolerate, and the populations crashed immediately after an outbreak.

In future agricultural systems, carabids may face prey populations developing on genetically modified crops with artificial pest defences incorporated. Like natural defences, these may create tritrophic effects by interfering with the predator–herbivore interactions higher up in the food chain, whether this is due to sequestration or just to altered chemical composition of the herbivore. Jørgensen and Lövei (1999) simulated this situation by incorporating a proteinase-inhibitor into the food of a

caterpillar, and subsequently offered the caterpillar to a carabid, *Harpalus affinis*. They found a significantly reduced feeding rate on the modified food compared to controls.

Dietary mixing

Generalist consumers have often been found to respond positively to offerings of mixed diet compared to diets of a single food type (Waldbauer and Friedman, 1991). It is generally assumed that the benefit obtained is due either to a higher diversity of nutrients in the mixed diet, or to the better possibilities for self-selection of the optimal nutrient balance with a diverse availability. So far, there are very few studies testing these effects for carabid beetles, representing only few of the feeding guilds. In a spider, Toft and Wise (1999a) found that no or negative effects of prey mixing were more frequent than positive effects, depending on the quality of the diet constituents, and similar results may pertain to carabids (cf. *Table 3.1*). So far, mostly neutral and positive mixing effects have been published, and no case of negative mixing effects has been reported from carabid beetles. Wallin *et al.* (1992) found both egg size and rate of egg laying in *Bembidion lampros* to be greater when fed a mixed diet of aphids and cat food, compared to the monotypic diets. In two other species, no differences were found. In *Agonum dorsale*, fecundity was greatly increased by the mixed diet (fruit flies, aphids and earthworm) compared to single-prey diets of each constituent (Bilde and Toft, 1994). In the granivore *Amara similata*, a mixed-seed diet improved female fecundity but not larval development compared to the best single-seed diet (Jørgensen and Toft, 1997). Mixing of seeds and insects, however, made no improvement compared to the mixed-seed diet. In *H. rufipes*, the mixed-seed diet gave only the same rate of larval development as the best of its elements (Jørgensen and Toft, 1997b).

Effects of diet quality may not only influence the consumer itself, they may also be transmitted to the consumer's offspring as maternal effects. Thus, under identical conditions, larvae of *Amara similata* whose mothers were kept on a monotonous seed diet survived better than larvae whose mothers had been kept on the higher-quality, mixed-seed diet. Thus, high value to the female corresponded to low performance of the young. Most likely, females on the monotypic diets laid fewer but larger eggs than females on the high-quality, mixed diets (cf. Wallin *et al.*, 1992).

If dietary mixing is advantageous, it means that the single food types alone are not high-quality. It can be hypothesized that the essential foods to which members of a feeding guild are particularly adapted are nutritionally more complete than supplementary foods. If this holds true, it can be predicted that diets should be more mixed (have more complementary constituents in order to compose a complete diet) if it consists of supplementary food types than if it consists of essential foods. An alternative hypothesis may be that supplementary foods contain more defensive deterrents and toxins than essential foods, both being equally variable with respect to nutrient composition. In this case, all foods potentially may complement each other to produce the same benefit, but inclusion of toxic food may interfere with the predator's utilization of essential food and thus prevent it from obtaining a benefit. At this stage, it is not possible to evaluate these alternatives as far as carabid beetles are concerned. Results from spiders are in best agreement with the second hypothesis (Toft and Wise, 1999ab).

Food limitation

Evidence that carabid beetles are limited by food availability in many habitats, including agricultural fields, comes from different sources. Granivorous species have repeatedly been demonstrated to respond positively to increased weed density in agricultural fields (de Snoo *et al.*, 1995; Holland *et al.*, 1999), indicating that populations are limited by seed availability (or they may be seeking out the environmental conditions provided by the weeds). For the insectivore *Agonum dorsale*, Bilde and Toft (1998) used the degree of hunger of field-caught animals to compare seasonal variations in food limitation. This index is better than direct measurement of prey availability because it also accounts for seasonal variations in food demand.

Food limitation in the early spring when carabids invade agricultural fields from surrounding uncultivated habitats may be serious. Bilde and Toft (1998) estimated an average degree of hunger equivalent to 2–3 weeks of starvation at 20°C for *A. dorsale* in a winter wheat field in May. This is likely to have consequences for the reproductive rate of this spring breeding population and thus for its ability to affect immigrating aphids later in the season (cf. Sunderland, this volume). Since aphids are low-quality food, aphid predation is unlikely to increase significantly, even if the carabids aggregate where the aphids are plentiful (cf. Monsrud and Toft, 1999). Therefore, the efficacy of predator limitation of aphids can only be enhanced by finding ways to increase the amount of alternative food available to the predators, and in this way increase the number of predators in the field.

Exploitative competition

In line with the conclusions of Hengeveld (1980b), Dennison and Hodkinson (1983) stressed the high degree of dietary overlap among coexisting carabid and staphylinid species, implying potential competition for food also among species with different specializations. However, consideration of food value is also a necessity before potential competition can be deduced from food overlap. Our results (Jørgensen and Toft, 1997a,b) indicate that seed feeders (*Amara*, *Harpalus*) will not compete with generalist insectivores, in spite of high dietary overlap with these, because the insect part of the diet has little or no importance for their fitness, and the seed part of the diet probably has little importance for the fitness of insectivores. Reduced availability of supplementary food will therefore have little importance. Also, if supplementary prey is of low quality, individuals are not likely to aggregate where they occur in high densities, even if they are tolerant of consuming a lot. Only exploitative reduction of high-quality essential food types is likely to have potential competitive effects. We therefore believe that consideration of food value should be more explicitly incorporated in the definition of species' food niches.

Field experiments aimed at demonstrating competition between carabid species have concentrated on coexisting congenerics with not only a high dietary overlap, but presumably also very similar ranges of essential prey where it is thus most likely to occur. Lenski (1982, 1984) found evidence for improved foraging success and interspecific competition between two *Carabus* species following density manipulations. In another similar case, there was no evidence for exploitative food competition, in spite of significant food limitation of the involved species (Juliano, 1986).

Food value and pest limitation

Carabids have often been mentioned as potentially important predators on several agricultural or forest pests, e.g. aphids (Sunderland, 1975; Sunderland *et al.*, 1987), cabbage root fly eggs (Hughes, 1959; Coaker and Williams, 1963), wheat midges (Floate *et al.*, 1990), wireworms (Fox and MacLellan, 1956), codling moth larvae (Hagley *et al.*, 1982), cutworms (Frank, 1971), slugs (Symondson *et al.*, 1996; Bohan *et al.*, 2000) and gipsy moths (Weseloh, 1985). In most of these cases, natural control is exerted by the community of carabid beetles and other generalist predator species that have not specialized in preying on the pest. The probable exception is that of forest caterpillars, preyed upon by *Calosoma sycophanta* (Weseloh, 1985). Here, the prey seems to be a high-quality exclusive food for the predator. In the other cases, the pest is just one of a wide range of prey taken. Often, consumption of the pest is probably of little importance to predator fitness because it forms just a small fraction of its food intake (fly eggs), in some cases it may even be supplementary low-quality food for the beetles (aphids). In the latter situation, the feeding specializations of the predator may be more or less irrelevant for their impact on the pest. Even the granivorous species prey frequently on pest insects (e.g. aphids: Sunderland *et al.*, 1987; codling moth larvae: Hagley *et al.*, 1982), though this is of little benefit to them (Jørgensen and Toft, 1997a,b). If the beetles or their larvae are numerous, supplementary predation may anyway have a significant effect on the pest, even if there is no aggregating response, and individual feeding rate on the pest is low. In order for this to be true, the pest must have a specially vulnerable phase in the population cycle, as is the case with aphids, where even a numerically low predation rate at the aphid immigration period have consequences for subsequent population growth (see further Sunderland, this volume).

A comparable example was given by Lukasiewicz (1996), who pointed out that *P. melanarius*, in spite of a low frequency of earthworm predation, might be more important for reduction of earthworms than the earthworm specialist, *Carabus granulatus*, because of its high population densities. Granivore carabids may also have an impact on the seed population of plants whose seeds are highly preferred. Kjellson (1985) estimated that *Harpalus fuliginosus* removed 65% of the seed pool of *Carex pilulifera*. Despite this, effects on the plant population are doubtful.

Conclusion

Let us 'summarize' by listing some of the main open questions revealed by this review. The answers to some of these questions are very basic to our understanding of how carabids function in the biological communities.

- Which prey are essential high-quality food for the generalist insectivorous carabids in the field? Answering this question requires studies that combine quantitative research of field consumption with laboratory determinations of food value of potentially important prey types. We expect that studies are needed at the level of prey species (rather than families or orders).
- Is the essential prey of specialists also essential prey of corresponding generalists? For example, are the Collembola, to which the microarthropod specialists are particularly adapted, also high-quality food for the generalist insectivores?

Likewise, are the high-quality slugs of the mollusc specialists also high-quality food for the large generalist carnivores?

- How are specialist carabids adapted to overcome nutrient imbalances due to a one-sided diet? The evolution of diet specialization may be costly in terms of a trade-off in growth rate, fecundity or size due to nutritional imbalance. Can the performance of specialized predators be significantly improved by dietary mixing? Are the essential prey of specialists particularly rich in nutrients? Or have specialists adapted to cope with poor nutrient composition?
- Do generalist feeders have larger quantities of essential prey available than the specialists? Do generalist feeders have a wider range of essential prey species than the specialists, or are they generalists because they accept more intermediate- and low-quality food?
- What are the physiological mechanisms of feeding specialization? To what extent does it involve resistance against specific chemical constituents of prey, or depend on the compliment of digestive enzymes?
- What are the behavioural mechanisms of food selectivity for generalists and specialists? Do specialists initially accept a more narrow variety of food types than generalists? Do specialists develop aversions to unsuitable prey earlier than generalists?
- To what extent are carabids able to select a nutritionally optimal diet, or to compose an optimal mix of prey types containing deterrents or toxins? Can the degree of dietary mixing be behaviourally modified according to the nutritional condition of the individual?
- What is the role of non-essential food in the diets of (generalist) carabids? Some prey types (e.g. aphids) may contribute to the fitness of a carabid, though only small amounts are consumed; others may be useless, in spite of a substantial consumption rate. The same prey may be valuable to some carabid species and without value to others, even if the latter consumes the most.
- Is food limited both in terms of quantity and quality in cultivated fields, and more so in conventionally managed than in organic fields?
- The ecological role of carabid larvae. The need for more detailed studies of larval feeding habits has already been stressed. We have presented evidence that, at least in *Bembidion lampros*, several types of prey that are low quality to adults (e.g. aphids and some Collembola) may allow complete development of young, even as monotypic diets. These findings are likely to mean that larvae less easily develop aversions against these prey, and thus may be better able than the adults to respond functionally and numerically to increased densities; the numerical response has also been confirmed. Thus, larvae may not only have a very different role than the adults in the detritus-based food web of the soil, they may also be far more important as aphid antagonists than recognized so far.

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References

ALLEN, W.R. AND HAGLEY, E.A.C. (1982). Evaluation of immuno-electrosmophoresis on cellulose polyacetate for assessing predation of Lepidoptera (Tortricidae) by Coleoptera (Carabidae) species. *The Canadian Entomologist* **114**, 1047–1058.

ANDERSON, J.M. (1972). Food and feeding of *Notiophilus biguttatus* F. (Coleoptera: Carabidae). *Revue d'Ecologie et de Biologie du Sol* **9**, 177–184.

BAUER, T. (1981). Prey capture and structure of the visual space of an insect that hunts by sight on the litter layer (*Notiophilus biguttatus* F., Carabidae, Coleoptera). *Behavioural Ecology and Sociobiology* **8**, 91–97.

BAUER, T. (1982). Prey-capture in a ground-beetle larva. *Animal Behaviour* **30**, 203–208.

BAUER, T. (1985). Beetles which use a setal trap to hunt springtails: the hunting strategy and apparatus of *Leistus* (Coleoptera, Carabidae). *Pedobiologia* **28**, 275–287.

BAUER, T. AND KREDLER, M. (1988). Adhesive mouthparts in a ground beetle larva (Coleoptera, Carabidae, *Loricera pilicornis* F.) and their function during predation. *Zoologischer Anzeiger* **221**, 145–156.

BERNAYS, E.A. (1993). Aversion learning and feeding. In: *Insect learning*. Eds. D.R. Papaj and A.C. Lewis, pp 1–17. New York: Chapman & Hall.

BILDE, T. AND TOFT, S. (1994). Prey preference and egg production of the carabid beetle *Agonum dorsale*. *Entomologia Experimentalis et Applicata* **73**, 151–156.

BILDE, T. AND TOFT, S. (1997a). Limited predation capacity by generalist arthropod predators on the cereal aphid, *Rhopalosiphum padi*. *Organic Agriculture and Horticulture* **20**, 143–150.

BILDE, T. AND TOFT, S. (1997b). Consumption by carabid beetles of three cereal aphid species relative to other prey types. *Entomophaga* **42**, 21–32.

BILDE, T. AND TOFT, S. (1998). Quantifying food limitation of arthropod predators in the field. *Oecologia* **115**, 54–58.

BILDE, T. AND TOFT, S. (1999). Prey consumption and fecundity of the carabid beetle *Calathus melanocephalus* on diets of three cereal aphids: high consumption rates of low-quality prey. *Pedobiologia* **43**, 422–429.

BILDE, T. AND TOFT, S. (2000). Evaluation of prey for the spider *Dicymbium brevisetosum* Locket (Araneae: Linyphiidae) in single-species and mixed-species diets. *Ekológia (Bratislava)* **19** Suppl. 3, 9–18.

BILDE, T., AXELSEN, J.A. AND TOFT, S. (2000). The value of Collembola from agricultural soils as food for a generalist predator. *Journal of Applied Ecology* **37**, 672–683.

BOHAN, D.A., BOHAN, A.C., SYMONDSON, W.O.C., WILTSHIRE, C.W. AND HUGHES, L. (2000). Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology* **69**, 367–379.

BRANDMAYR, T.Z. (1990). Spermophagous (seed eating) ground beetles: first comparison of the diet and ecology of the Harpaline genera *Harpalus* and *Ophonus* (Col., Carabidae). In: *The role of ground beetles in ecological and environmental studies*. Ed. N.E. Stork, pp 307–316. Andover: Intercept.

BRYAN, K.M. AND WRATTEN, S.D. (1984). The responses of polyphagous predators to prey spatial heterogeneity: aggregation by carabid and staphylinid beetles to their aphid prey. *Ecological Entomology* **9**, 251–259.

BURAKOWSKI, B. (1986). The life-cycle and food preference of *Agonum quadripunctatum* (De Geer). In: *Feeding behaviour and accessibility of food for carabid beetles*. Eds. P.J. den Boer, L. Grüm and J. Szyszko, pp 35–39. Warsaw: Warsaw Agricultural University Press.

COAKER, T.H. AND WILLIAMS, D.A. (1963). The importance of some Carabidae and Staphylinidae as predators of the cabbage root fly, *Erioischia brassicae* (Bouché). *Entomologia Experimentalis et Applicata* **6**, 156–164.

CORNIC, J.F. (1973). Étude du régime alimentaire de trois espèces de carabiques et de ses variations en verger de pommiers. *Annales de la Societé Entomologique de France (N.S.)* **9**, 69–87.

DAJOZ, R. (1987). Le régimes alimentaire des coléoptères Carabidae. *Cahiers des Naturalistes, N.S.* **43**, 61–96.

DAVIES, M.J. (1953). The contents of the crops of some British carabid beetles. *Entomologist's Monthly Magazine* **89**, 18–23.

DAWSON, N. (1965). A comparative study of the ecology of eight species of fenland Carabidae (Coleoptera). *Journal of Animal Ecology* **34**, 299–314.

DEN BOER, P.J. (1986). Facts, hypotheses and models on the part played by food in the dynamics of carabid populations. In: *Feeding behaviour and accessibility of food for carabid beetles*. Eds. P.J. Den Boer, L. Grüm and J. Szyszko, pp 81–96. Warsaw: Warsaw Agricultural University Press.

DENNISON, D.F. AND HODKINSON, I.D. (1983). Structure of the predatory beetle community in a woodland soil ecosystem. I. Prey selection. *Pedobiologia* **25**, 109–115.

DE SNOO, G.R., VAN DER POLL, R.J. AND DE LEEUW, J. (1995). Carabids in sprayed and unsprayed crop edges of winter wheat, sugar beet and potatoes. In: *Arthropod natural enemies in arable land. I Density, spatial heterogeneity and dispersal*. Eds. S. Toft and W. Riedel, pp 199–211. Århus: Aarhus University Press.

DETTNER, K., SCHEUERLEIN, A., FABIAN, K., SCHULZ, S. AND FRANCKE, W. (1996). Chemical defence in the giant springtail Tetrodontophora bielanensis (Waga) (Insecta: Collembola). *Journal of Chemical Ecology* **22**, 1051–1074.

DIGWEED, S.C. (1993). Selection of terrestrial gastropod prey by cychrine and pterostichine ground beetles (Coleoptera: Carabidae). *The Canadian Entomologist* **125**, 463–472.

DREISIG, H. (1981). The rate of predation and its temperature dependence in a tiger beetle, *Cicindela hybrida*. *Oikos* **36**, 196–202.

ERNSTING, G. AND JANSEN, J.W. (1978). Interspecific and intraspecific selection by the predator *Notiophilus biguttatus* F. (Carabidae) concerning two collembolan prey species. *Oecologia* **33**, 173–183.

ERNSTING, G., JAGER, J.C., VAN DER MEER, J. AND SLOB, W. (1985). Locomotory activity of a visually hunting carabid beetle in response to non-visual prey stimuli. *Entomologia Experimentalis et Applicata* **38**, 41–47.

ERNSTING, G., ISAAKS, J.A. AND BERG, M.P. (1992). Life cycle and food availability indices in *Notiophilus biguttatus* (Coleoptera, Carabidae). *Ecological Entomology* **17**, 33–42.

EVANS, M.E.G. AND FORSYTHE, T.G. (1984). A comparison of adaptation to running, pushing and burrowing in some adult Coleoptera: especially Carabidae. *Journal of Zoology, London* **202**, 513–534.

EVANS, M.E.G. AND FORSYTHE, T.G. (1985). Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of Zoology, London* **206**, 113–143.

FLOATE, K.D., DOANE, J.F. AND GILLOTT, C. (1990). Carabid predators of the wheat midge (Diptera, Cecidomyiidae) in Sakatchewan. *Environmental Entomology* **19**, 1503–1511.

FORBES, S.A. (1883). The food relations of the Carabidae and Coccinellidae. *Illinois State Laboratory, Natural History Bulletin* **1**, 33–64.

FORSYTHE, T.G. (1982a). Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). *The Coleopterist's Bulletin* **36**, 26–73.

FORSYTHE, T.G. (1982b). Qualitative analyses of certain enzymes of the oral defence fluids of *Pterostichus madidus* (F.), including a list of other carabid beetles which produce oral defence fluids. *Entomologist's Monthly Magazine* **118**, 1–5.

FORSYTHE, T.G. (1983). Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). *Zoological Journal of the Linnean Society* **79**, 319–376.

FORSYTHE, T.G. (1987). The relationship between body form and habit in some Carabidae (Coleoptera). *Journal of Zoology, London* **211**, 643–666.

FORSYTHE, T.G. (1991). Feeding and locomotory functions in relation to body form in five species of ground beetle (Coleoptera: Carabidae). *Journal of Zoology, London* **223**, 233–363.

FOX, C.J.S. AND MACLELLAN, C.R. (1956). Some Carabidae and Staphylinidae shown to feed on a wireworm, *Agriotes sputator* (L.), by the Precipitin test. *The Canadian Entomologist* **88**, 228–231.

FRANK, J.H. (1971). Carabidae (Coleoptera) as predators of the red-backed cutworm (Lepidoptera: Noctuidae) in Central Alberta. *The Canadian Entomologist* **103**, 1039–1044.

GOLDSCHMIDT, H. AND TOFT, S. (1997). Variable degrees of granivory and phytophagy in insectivorous carabid beetles. *Pedobiologia* **41**, 521–525.

GREENE, A. (1975). Biology of the five species of Cychrini (Coleoptera: Carabidae) in the steppe region of Southeastern Washington. *Melanderia* **19**, 1–41.

GOULET, H. (1976). A method for rearing ground beetles (Coleoptera: Carabidae). *The Coleopterist's Bulletin* **30**, 33–36.

HAGLEY, E.A.C., HOLLIDAY, N.J. AND BARBER, D.R. (1982). Laboratory studies of the food preferences of some orchard carabids (Coleoptera: Carabidae). *The Canadian Entomologist* **114**, 431–437.

HENGEVELD, R. (1980a). Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): a review. *Netherland Journal of Zoology* **30**, 555–563.

HENGEVELD, R. (1980b). Polyphagy, oligophagy, and food specialization in ground beetles (Coleoptera, Carabidae). *Netherland Journal of Zoology* **30**, 564–584.

HENGEVELD, R. (1980c). Food specialization in ground beetles: an ecological or a phylogenetic process? (Coleoptera, Carabidae). *Netherland Journal of Zoology* **30**, 585–594.

HENGEVELD, R. (1981). The evolutionary relevance of feeding habits of ground beetles (Coleoptera: Carabidae). *Entomologica Scandinavica Supplement* **15**, 305–315.

HINTZPETER, U. AND BAUER, T. (1986). The antennal trap of the ground beetle *Loricera pilicornis*: a specialization for feeding on Collembola. *Journal of Zoology, London* **208**, 615–630.

HOLLAND, J.M., PERRY, J.N. AND WINDER, L. (1999). The within-field spatial and temporal distribution of arthropods in winter wheat. *Bulletin of Entomological Research* **89**, 499–513.

HOPKIN, S.P. (1997). *Biology of the springtails*. Oxford: Oxford University Press.

HORTON, D.R. AND REDAK, R.A. (1993). Further comments on analysis of covariance in insect dietary studies. *Entomologia Experimentalis et Applicata* **69**, 263–275.

HOUSTON, W.W.K. (1981). The life cycle and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst (Col.: Carabidae) on moorland in Northern England. *Ecological Entomology* **6**, 263–271.

HUGHES, R.D. (1959). The natural mortality of *Erioischia brassicae* (Bouché) during the egg stage of the first generation. *Journal of Animal Ecology* **28**, 343–357.

JASPAR-VERSALI, M.F. AND JEUNIAUX, C. (1987). L'équipement enzymatique digestif des Carabes envisagé sous l'angle de leur nich écologique. *Revue d'Écologie et de Biologie du Sol* **24**, 541–547.

JASPAR-VERSALI, M.F., GOFFINET, G. AND JEUNIAUX, C. (1987). The digestive system of adult carabid beetles: an ultrastructural and histoenzymological study. *Acta Phytopathologica Entomologica Hungariae* **22**, 375–382.

JØRGENSEN, H.B. AND LÖVEI, G.L. (1999). Tri-trophic effect on predator feeding: consumption by the carabid *Harpalus affinis* of *Helothis armigera* caterpillars fed on proteinase inhibitor-containing diet. *Entomologia Experimentalis et Applicata* **93**, 113–116.

JØRGENSEN, H.B. AND TOFT, S. (1997a). Role of granivory and insectivory in the life cycle of the carabid beetle *Amara similata*. *Ecological Entomology* **22**, 7–15.

JØRGENSEN, H.B. AND TOFT, S. (1997b). Food preference, diet dependent fecundity and larval development in *Harpalus rufipes* (Coleoptera: Carabidae). *Pedobiologia* **41**, 307–315.

JULIANO, S.A. (1986). A test for competition for food among adult *Brachinus* spp. (Coleoptera: Carabidae). *Ecology* **67**, 1655–1664.

KIELTY, J.P., ALLEN-WILLIAMS, L.J., UNDERWOOD, N. AND EASTWOOD, E.A. (1996).

Behavioural responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. *Journal of Insect Behaviour* **9**, 237–250.

KIELTY, J.P., ALLEN-WILLIAMS, L.J. AND UNDERWOOD, N. (1999). Prey preferences of six species of Carabidae (Coleoptera) and one Lycosidae (Araneae) commonly found in UK arable crop fields. *Journal of Applied Entomology* **123**, 193–200.

KING, P.E. AND STABINS, V. (1971). Aspects of the biology of a strand-living beetle, *Eurynebria complanata* (L.). *Journal of Natural History* **5**, 17–28.

KJELLSON, G. (1985). Seed fate in a population of *Carex pilulifera* L. II. Seed predation and its consequences for dispersal and seed bank. *Oecologia* **67**, 424–429.

KOEHLER, H. (1976). Nahrungsspektrum und Nahrungskonnex von *Pterostichus oblongopunctatus* (F.) und *Pterostichus metallicus* (F.) (Coleoptera, Carabidae). *Verhandlungen der Gesellschaft für Ökologie, Göttingen* **1976**, 103–111.

LANG, A. AND GSÖDL, S. (2001). Prey vulnerability and active predator choice as determinants of prey selection: a carabid beetle and its aphid prey. *Journal of Applied Entomology* **125**, 53–61.

LAROCHELLE, A. (1990). *The food of carabid beetles.* Québec: Fabreries, Supplement 5, Association des Entomologistes Amateurs du Québec.

LENSKI, R.E. (1982). Effects of forest cutting on two *Carabus* species: evidence for competition for food. *Ecology* **63**, 1211–1217.

LENSKI, R.E. (1984). Food limitation and competition: a field experiment with two *Carabus* species. *Journal of Animal Ecology* **53**, 203–216.

LINDROTH, C.H. (1949). *Die Fennoskandischen Carabidae. Eine tiergeographische Studie. I. Spezieller Teil.* Goteborg: Elanders Boktryckeri Aktiebolag.

LINDROTH, C.H. (1992). *Ground beetles (Carabidae) of Fennoscandia: a zoogeographic study: Part 1. Specific knowledge regarding the species.* Andover: Intercept.

LOREAU, M. (1983a). Le régime alimentaire de *Abax ater* Vill. (Coleoptera, Carabidae). *Acta Oecologia, Oecologia Generalis* **4**, 253–263.

LOREAU, M. (1983b). Le régime alimentaire de huit carabides (Coleoptera) communs en milieu forestier. *Acta Oecologia, Oecologia Generalis* **4**, 331–343.

LOREAU, M. (1984). Étude expérimentale de l'alimentation de *Abax ater* Villers, *Carabus problematicus* Herbst et *Cychrus attenuatus* Fabricius (Coeloptera, Carabidae). *Annales de la Societé Royale Zoologique de Belge* **114**, 227–240.

LÖVEI, G.L. AND SUNDERLAND, K.D. (1996). Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**, 231–256.

LUFF, M.L. (1974). Adult and larval feeding habits of *Pterostichus madidus* (F.) (Coleoptera: Carabidae). *Journal of Natural History* **8**, 403–409.

LUFF, M.L. (1980). The biology of the ground beetle *Harpalus rufipes* in a strawberry field in Northumberland. *Annals of Applied Biology* **94**, 153–164.

LUFF, M.L. (1987). Biology of polyphagous ground beetles in agriculture. *Agricultural Zoology Reviews* **2**, 237–278.

LUKA, H., PFIFFNER, L. AND WYSS, E. (1998). *Amara ovata* und *A. similata* (Coleoptera, Carabidae), zwei phytophage Laufkäferarten in Rapsfeldern. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **71**, 125–131.

LUKASIEWICZ, J. (1996). Predation by the beetle *Carabus granulatus* L. (Coleoptera, Carabidae) on soil macrofauna in grassland and drained peats. *Pedobiologia* **40**, 364–376.

MESSER, C. AND DETTNER, K. (1997). Inhaltstoffe von Collembolen – spurenanalytische Untersuchungen und Biotests. *Mitteilungen der Deutschen Gesellschafft für Allgemeine and Angewandte Entomologie* **11**, 465–468.

MESSER, C., WALTHER, J., DETTNER, K. AND SCHULZ, S. (2000). Chemical deterrents in podurid Collembola. *Pedobiologia* **44**, 310–220.

MITCHELL, B. (1963). Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). I. Life cycle and feeding behaviour. *Journal of Animal Behaviour* **32**, 289–299.

MONSRUD, C. AND TOFT, S. (1999). The aggregative numerical response of polyphagous predators to aphids in cereal fields: attraction to what? *Annals of Applied Biology* **134**, 265–270.

PEARSON, D.L. AND MURY, E.J. (1979). Character divergence and convergence among tiger beetles (Coleoptera: Cicindelidae). *Ecology* **60**, 557–566.

POLLET, M. AND DESENDER, K. (1985). Adult and larval feeding ecology in *Pterostichus melanarius* Ill. (Coleoptera, Carabidae). *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **50**, 581–594.

POLLET, M. AND DESENDER, K. (1986). Prey selection in carabid beetles (Col., Carabidae): are diel activity patterns of predators and prey synchronized? *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **51**, 957–971.

POLLET, M. AND DESENDER, K. (1987). Feeding ecology of grassland-inhabiting carabid beetles (Carabidae, Coleoptera) in relation to the availability of some prey groups. *Acta Phytopathologica Entomologica Hungariae* **22**, 223–246.

POLLET, M. AND DESENDER, K. (1988). Quantification of prey uptake in pasture inhabiting carabid beetles. *Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent* **53**, 1119–1129.

POLLET, M. AND DESENDER, K. (1989). Prey uptake in subdominant, small to medium-sized carabid beetles from a pasture ecosystem. *Mededelingen van de Faculteit Landbouwetenschappen Rijksuniversiteit Gent* **54**, 809–822.

RAUBENHEIMER, D. AND SIMPSON, S.J. (1992). Analysis of covariance: an alternative to nutritional indices. *Entomologia Experimentalis et Applicata* **62**, 221–231.

SCHELVIS, J. AND SIEPEL, H. (1988). Larval food spectra of *Pterostichus oblongopunctatus* and *P. rhaeticus* in the field (Coleoptera: Carabidae). *Entomologia Generalis* **13**, 61–66.

SCHERNEY, F. (1959). *Unsere Laufkäfer.* Wittenberg: A. Ziemsen Verlag.

SCHERNEY, F. (1961). Beiträge zur Biologie und ökonomische Bedeutung räuberisch lebender Käferarten. *Zeitschrift für angewandte Entomologie* **48**, 163–175.

SCHREMMER, F. (1960). Beitrag zur Biologie von *Ditomus clypeatus* Rossi, eines körnersammelden Carabiden. *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* **12**, 140–145.

SHAROVA, I.CH. (1981). *Life forms of carabids (Coleoptera, Carabidae).* Moscow: Nauka Publishers.

SKUHRAVÝ, V. (1959). Die Nahrung der Feldcarabiden. *Acta Societatis Entomologicae Cechosloveniae* **56**, 1–18.

SLANSKY, F. AND PANIZZI, A.R. (1986). Nutritional ecology of seed-sucking insects. In: *Nutritional ecology of insects, mites, spiders, and related invertebrates.* Eds. F. Slansky and J.G. Rodriguez, pp 283–320. New York: John Wiley & Sons.

SNIDER, R.M. (1984). Diplopoda as food for Coleoptera: laboratory experiments. *Pedobiologia* **26**, 197–204.

SØRENSEN, O.F. (1996). The effects of day length, temperature and prey type on food consumption by *Bembidion lampros* and *Tachyporus hypnorum*. Masters Thesis. Department of Zoology, Aarhus University, Århus.

SOTA, T. (1984). Long adult life span and polyphagy of a carabid beetle, *Leptocarabus kumagaii* in relation to reproduction and survival. *Researches on Population Ecology* **26**, 389–400.

SOTA, T. (1985). Activity patterns, diets and interspecific interactions of coexisting spring and autumn breeding carabids: *Carabus yaconinus* and *Leptocarabus kumagaii* (Coleoptera, Carabidae). *Ecological Entomology* **10**, 315–324.

SPENCE, J.R. AND SUTCLIFFE, J.F. (1982). Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). *Canadian Journal of Zoology* **60**, 2382–2394.

SPIELES, D.J. AND HORN, D.J. (1998). The importance of prey for fecundity and behaviour in the gypsy moth (Lepidoptera: Lymantriidae) predator *Calosoma sycophanta* (Coleoptera: Carabidae). *Environmental Entomology* **27**, 458–462.

SUNDERLAND, K.D. (1975). The diet of some predatory arthropods in cereal crops. *Journal of Applied Ecology* **12**, 507–515.

SUNDERLAND, K.D. AND SUTTON, S.L. (1980). A serological study of arthropod predation on woodlice in a dune grassland ecosystem. *Journal of Animal Ecology* **49**, 987–1004.

SUNDERLAND, K.D., CROOK, N.E., STACEY, D.L. AND FULLER, B.J. (1987). A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology* **24**, 907–933.

SYMONDSON, W.O.C. (1993). The effects of crop development upon slug distribution and control by *Abax parallelepipedus* (Coleoptera: Carabidae). *Annals of Applied Biology* **123**, 449–457.

SYMONDSON, W.O.C. (1994). The potential of *Abax parallelepipedus* (Coleoptera: Carabidae) for mass breeding as a biological control agent against slugs. *Entomophaga* **39**, 323–333.

SYMONDSON, W.O.C. (1997). Does *Tandonia budapestensis* (Mollusca: Pulmonata) contain toxins? Evidence from feeding trials with the slug predator *Pterostichus melanarius* (Coleoptera: Carabidae). *Journal of Molluscan Studies* **63**, 541–545.

SYMONDSON, W.O.C. (in press). Coleoptera (Carabidae, Drilidae, Lampyridae and Staphylinidae). In: *Natural enemies of terrestrial molluscs*. Ed. G.M. Barker. Oxford: CAB International.

SYMONDSON, W.O.C. AND LIDDELL, J.E. (1993). Differential antigen decay rates during digestion of molluscan prey by carabid predators. *Entomologia Experimentalis et Applicata* **69**, 277–287.

SYMONDSON, W.O.C., GLEN, D.M., WILTSHIRE, C.W., LANGDON, C.J. AND LIDDELL, J.E. (1996). Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *Journal of Applied Ecology* **33**, 741–753.

SYMONDSON, W.O.C., GLEN, D.M., ERICKSON, M.L., LIDDELL, J.E. AND LANGDON, C.J. (2000). Do earthworms help to sustain the slug predator *Pterostichus melanarius* (Coleoptera: Carabidae) within crops? Investigations using a monoclonal antibody-based detection system. *Molecular Ecology* **9**, 1279–1292.

TERRA, W.W., FERREIRA, C., JORDAO, B.P. AND DILLON, R.J. (1996). Digestive enzymes. In: *Biology of the insect midgut*. Eds. M.J. Lehane and P.F. Billingsley, pp 153–194. London: Chapman & Hall.

THIELE, H.-U. (1977). *Carabid beetles in their environment*. Berlin: Springer-Verlag.

TOD , M.E. (1973). Notes on beetle predators on molluscs. *The Entomologist* **106**, 196–201.

TOFT, S. (1995). Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology* **32**, 552–560.

TOFT, S. (1996). Indicators of prey quality for arthropod predators. In: *Arthropod natural enemies in arable land. II. Survival, reproduction and enhancement*. Eds. C.J.H. Booij and L.J.M.F. den Nijs, pp 107–116. Århus: Aarhus University Press.

TOFT, S. (1997). Acquired food aversion of a wolf spider to three cereal aphids: intra- and interspecific effects. *Entomophaga* **42**, 63–69.

TOFT, S. AND WISE, D.H. (1999a). Growth, development and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* **119**, 191–197.

TOFT, S. AND WISE, D.H. (1999b). Behavioural and ecophysiological responses of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* **119**, 198–207.

TRAUTNER, J. (1984). Zur Verbreitung und Ökologie der *Dromius*-Arten (Coleoptera, Carabidae) in Württemberg. *Jahreshefte der Gesellschaft für Naturkunde in Württemberg* **139**, 211–215.

TRAUTNER, J., GEISSLER, S. AND SETTELE, J. (1988). Zur Verbreitung und Ökologie des Laufkäfers *Diachromus germanus* (Linne 1758) (Col., Carabidae). *Mitteilungen der Entomologischen Vereins Stuttgart* **23**, 86–105.

VAJE, S.V., MOSSAKOWSKI, D. AND GABEL, D. (1984). Temporal, intra- and interspecific variation of proteolytic enzymes in carabid-beetles. *Insect Biochemistry* **14**, 313–320.

WALDBAUER, G.P. (1968). The consumption and utilization of food by insects. *Advances in Insect Physiology* **5**, 229–288.

WALDBAUER, G.P. AND FRIEDMAN, S. (1991). Self-selection of optimal diets by insects. *Annual Review of Entomology* **36**, 43–63.

WALLIN, H. (1988). Mandible wear in the carabid beetle *Pterostichus melanarius* in relation to diet and borrowing behaviour. *Entomologia Experimentalis et Applicata* **48**, 43–50.

WALLIN, H., CHIVERTON, P.A., EKBOM, B.S. AND BORG, A. (1992). Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomologia Experimentalis et Applicata* **65**, 129–140.

WESELOH, R.M. (1985). Changes in population size, dispersal behaviour, and reproduction of *Calosoma sycophanta* (Coleoptera: Carabidae), associated with changes in gipsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), abundance. *Environmental Entomology* **14**, 370–377.

WESELOH, R.M. (1993). Adult feeding affects fecundity of the predator *Calosoma sycophanta* (Col.: Carabidae). *Entomophaga* **38**, 435–439.

WHEATER, C.P. (1988). Predator-prey size relationships in some Pterostichini (Coleoptera: Carabidae). *The Coleopterist's Bulletin* **42**, 237–240.

WHEATER, C.P. (1989). Prey detection by some predatory Coleoptera (Carabidae and Staphylinidae). *Journal of Zoology, London* **218**, 171–185.

WINDER, L., PERRY, J.N. AND HOLLAND, J.M. (1999). The spatial and temporal distribution of the grain aphid *Sitobion avenae* in winter wheat. *Entomologia Experimentalis et Applicata* **93**, 275–288.

ZHAVORONKOVA, T.N. (1969). Certain structural peculiarities of the Carabids in relation to their feeding habits. *Entomological Review* **48**, 462–471.